IN SITU OBSERVATIONS OF FEEDING BEHAVIOR
OF THECOSOME PTEROPOD MOLLUSCS

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ABSTRACT

Recent *in situ* observations of thecosome pteropods were made during five cruises in tropical, temperate, and arctic waters of the North Atlantic Ocean, and during one astral summer season in Antarctic waters. The long quiescent periods employed by thecosomes to fish their mucous feeding webs and the apparent lack of a pumping mechanism to move water through the web suggests they rely on contact trapping of large, motile prey. Species of *Cavolinia* and *Diacria* were estimated to remain in one location for at least 35 min to fish sequential webs. The external spherical webs used by euthecosomes and their ability to rapidly ingest them appear to be a unique feeding method among plankton that utilize mucous feeding structures. All euthecosomes observed during night dives entrapped numerous small crustaceans as the webs were withdrawn, and all specimens diver-collected at night contained small copepods in their guts. Crustaceans also accounted for up to 25% by volume of the gut contents of *Limacina helicina* (Phipps) preserved *in situ* in arctic waters during July and August, 1988. Individuals of a given species use webs of comparable dimensions in different water masses. Based on the observed feeding strategies and on the common ingestion of copepods by arctic *Limacina* and by temperate and tropical cavoliniid species, carnivory can not be precluded as a primary feeding habit for the Thecosomata.

The Thecosomata comprise an order of common opisthobranch gastropods which exist in the holoplankton by means of parapodia for rapid swimming and by the use of large, external mucous webs to collect food (Lalli and Gilmer, 1989). Their feeding habits depend on buoyancy control and passive drifting. Consequently, they have greatly reduced the wall thickness of their external shell or replaced it with internal gelatinous conchae. They have no gills which can function for food gathering and resemble vermetid prosobranchs (Hughes and Lewis, 1974; Hughes, 1978) by using cilia on the surfaces of the mantle and footlobes to manipulate their feeding webs. Much of their behavior remains obscure due to their remote habitat, and the difficulty of observing them in an undisturbed state. In addition, their fragility makes collection of undamaged specimens difficult. Even carefully collected individuals display abnormal behavior in the laboratory where they only survive for brief periods.

Using blue water scuba techniques (Hamner, 1975) to observe undisturbed thecosomes has been the most useful means to study their feeding habits. The feeding webs are usually so fragile and transparent that they are only visible in daylight with bright strobe lighting or by the delicate application of carmine particles to the web surfaces (Gilmer and Harbison, 1986). The euthecosomes *(Limacina, Creseis, Styliola, Hyalocylis, Clio, Cavolinia, Diacria)* use spherical webs attached directly to the ciliated footlobes on the wings. The pseudothecosome genera *(Peraclis, Cymbulia, Corolla, Gleba)* use large flat or funnel shaped webs that float above the wingplate and are attached to the animal by a proboscis composed of the footlobes. Thecosomes are extremely sensitive to turbulence and, at the slightest provocation, will abandon their feeding activity with rapid escape swimming. Although the abandoned webs are left floating intact, their transparent and fragile nature have thus far made it impossible to sample them quantitatively.

Information on thecosome diet is limited to a few qualitative descriptions of gut contents, fecal pellets, and web fragments (see review in Lalli and Gilmer, 1989). Based on these studies, thecosomes appear to be indiscriminate omnivores ingesting all size categories of prey from 1 μm bacteria to copepods as large as 3 mm in length [seen in *Limacina helicoides* Jeffreys, Gilmer (pers. obs.)]. Thecosomes, however, are often categorized solely as herbivores (e.g. Morton, 1954; Silver and Bruland, 1981; Foster,

1987; Boysen-Ennen and Piatkowski, 1988) since many phytoplankton cells are captured and ingested with the web, and are prevalent in the fecal pellets. Herbivory is also considered synonymous with mucous suspension feeding (Jorgensen, 1966). This label, however, ignores a much broader diet that often includes many protozoan and zooplankton prey items (e.g. Richter, 1977, 1983; Ishimaru et al., 1988; Lalli and Gilmer, 1989) and seems generally inappropriate to describe their feeding strategy. Although no detailed studies exist to document the relative frequency of the various prey fractions, the external web (Gilmer, 1972, 1974; Gilmer and Harbison, 1986) provides an obvious trapping mechanism for fast swimming organisms. From mid-July to mid-August, 1988, metazoan zooplankton comprised an average of 45% by volume of items in the guts of 28 subarctic *Limacina helicina* (Phipps) preserved *in situ* (Gilmer and Harbison, unpub. data).

This paper describes observations, made with the use of scuba, of undisturbed thecosome individuals. These observations, some lasting up to 15 min, expand on previous observations (Gilmer, 1972; Gilmer and Harbison, 1986) and suggest ways that feeding webs could be produced, fished, and ingested. The term "mucous trapper" (Fallensteller), suggested by Richter (1977), is the most descriptive term relating to thecosome feeding behavior.

MATERIALS AND METHODS

Thecosome pteropods were observed and collected in hand-held glass jars by scuba divers during four cruises in the tropical and subtropical North Atlantic Ocean in May through August, 1986 (R/V "Oceanus" cruises 176, 177) in March, April, July and and August 1987 (R/V "Oceanus" cruises 184, 191), in the arctic and subarctic Atlantic Ocean in July and August, 1988 (R/V "Endeavor" cruise, 182), and under sea ice in McMurdo Sound, Antarctica in November 1987. Individual thecosomes were observed and photographed for up to 15 min in the upper 30 m of the water column using standard blue water techniques (Hamner, 1975). To make feeding webs more visible, I used either carmine dye dispensed from a plastic squeeze bottle or strobe lighting. On night dives the absence of ambient light made webs easily visible with diving lights.

Photographs were taken with a Nikonos V underwater camera fitted with 1:1 or 1:2 close-up lenses and backlit from 10 to 30 cm with one or two Nikonos SB-103 underwater strobes. Either Kodak Panatomic X, Technical Pan black and white film, or Kodachrome 64 color films were used. Some individuals were photographed in successive intervals of 20 to 30 sec to record feeding sequences. Web diameters were estimated to the nearest 10 mm from field photographs. Shell dimensions were measured to the nearest 0.2 mm using a dissecting microscope and ocular micrometer. Activity of arctic *Limacina helicina* was measured by a diver swimming horizontally through dense populations and randomly counting whether individuals were motionless or swimming. Counts were made until 10 swimming individuals were observed.

RESULTS

LIMACINA HELICINA (LIMACINIDAE: EUTHECOSOMATA)

Limacina helicina retains its largest known size in subarctic Atlantic waters (Lalli and Gilmer, 1989). I measured feeding webs (Fig. 1a) up to 60 mm in diameter on specimens with 12.2 mm diameter shells (Table 1). *L. helicina antarctica* Woodward with shells measuring 4.6 mm in diameter (Table 1), fed from webs with estimated diameters of 20 mm. *L. helicina* is very sensitive to turbulence and usually abandons its feeding web in the presence of a diver. Careful placement of a camera framer around the animal can cause it to simply draw in the web. It is deflated like a balloon and appears to be drawn in dorsally between the wings near the large pallial opening (Fig. 1b). The web is withdrawn solely by ciliary actions in 15 to 30 sec.

Web production was not observed, but could be associated with a curious somersaulting behavior (Fig. 2) that is displayed by all of the euthecosome species I have observed. This behavior always takes place when swimming animals switch to a motionless, feeding posture (Fig. 1a). The animal slows its swimming speed, but at the same time increases wing motion and moves in a small arch roughly similar in dimension to its feeding web. At the apex, the animal moves in quick back and forth twists while continuing its path. Near the bottom of the arch when the shell is situated above the wings, the body quickly reserves position leaving the wings extended uppermost. Swimming motion stops immediately and the animal now hangs motionless in the water. The entire somersaulting sequence takes from eight to twelve sec to complete in all species that I have observed. *Limacina helicina* and *L. retroversa* (Fleming) sink slightly after somersaulting, but attain neutral buoyancy within 5 sec. This condition then lasts for at least eight min (the longest observation period), and is the only period when I have observed feeding webs in place. Neutral buoyancy, however, is also displayed by mating couples with no apparent aid from feeding webs or other mucus structures.

On cruise "Endeavor" 182 *Limacina helicina* occurred in surface waters in a distinct layer between 5 and 28 m. More than 97% of the individuals I surveyed (n= 1200) were neutrally buoyant and motionless in their feeding posture. This percentage was similar on all dives made between 0800 hr and 1900 hr at various stations over 27 days. Feeding individuals that were occasionally bumped by swimming *Limacina* showed no reaction to the contact and continued their quiescent posture. Several *Limacina* were even pulled a short distance in the water when the intruder became entangled in the web. Similar passive behavior by other feeding *L. helicina* was observed on four occasions when gammariid amphipods (> 5 mm body length) blundered into the pteropod web. The amphipods immediately broke free of the web. After their encounter with the amphipod, two of the *Limacina* swam off and the other two remained quiescent but did not appear to set new webs during two minutes of further observation.
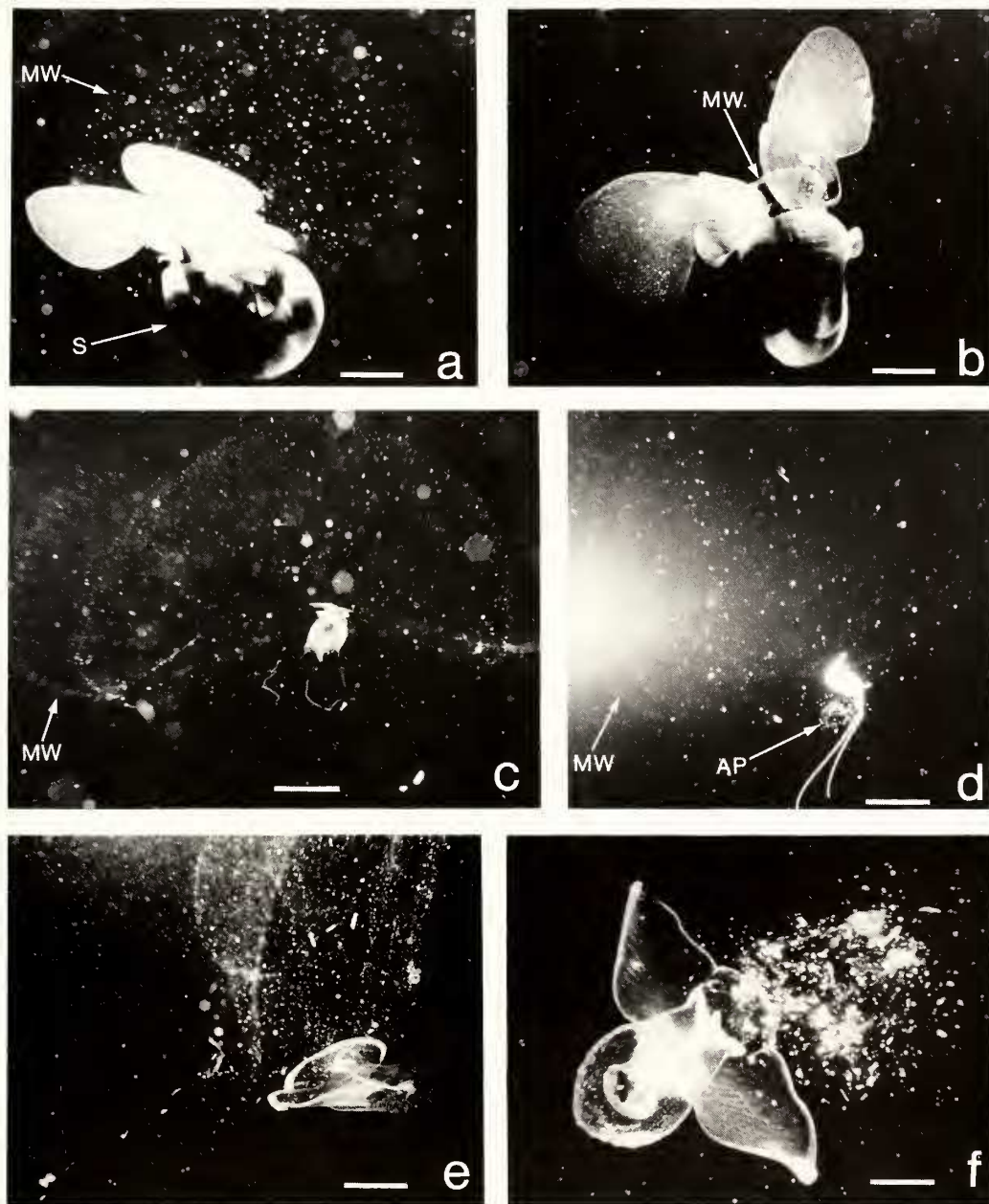
Fig. 1a. *Limacina helicina* in subarctic waters. Lateral view of individual in motionless feeding posture (S, shell; MW, mucous feeding web) (scale bar = 4 mm); **b,** *L. helicina,* dorsal view, in final stages of withdrawing feeding web (MW, mucous feeding web) (scale bar = 4 mm); **c,** *Cavolinia uncinata,* with extended mucous feeding web (MW) and no pseudofeces retained off the posterior shell margin (scale bar = 10 mm); **d,** *C. uncinata,* with extended feeding web (MW) and aggregated mass (AP) of pseudofeces and fecal pellets retained on the posterior shell margin indicating an earlier web was set in the same location (scale bar = 10 mm); **e,** *Corolla calceola* from northwestern Atlantic slope water with large mucous feeding web in place (scale bar = 25 mm); **f,** *C. calceola* with large mass of pseudofeces and feces after ingesting a feeding web (scale bar = 10 mm).

FAMILY CAVOLINIIDAE (EUTHECOSOMATA)

Within the upper 30 m, roughly 95% of the cavoliniids I observed maintained a quiescent feeding posture regardless of the time of day. The only exception to this is in turbulent mixing zones, such as langmuir cells or shear zones between warm and cold water masses (e.g. western edge of the Gulf Stream and northwestern slope water interface), where our dive team has encountered vertical currents of approximately 0.5 knot. Here cavoliniids are often abundant and rapidly swim to maintain their position, or are swept away in the current. These are exceptional circumstances, as most thecosomes retain their motionless, feeding posture within 3 m of

the surface on rough days (e.g. Beaufort wind force 7).

Cavoliniids rapidly ingest their feeding webs in a manner similar to *Limacina helicina*. Webs are collected ventrally on the large expanse of the footlobes and funnelled into the mouth as condensed strings. At night, I have routinely observed *Clio pyramidata* Linné and *Cuvierina columnella* (Rang) withdraw their largest webs (Table 1) in 15 sec. Cavoliniids also display variable escape responses to the presence of a diver (Gilmer and Harbison, 1986). At one extreme of their behavior, individuals will flee from a small hand motion initiated up to 3 m away. Conversely, they will sometimes allow a diver to touch them several times before an escape response is induced. This sporadic escape behavior is characteristic of all thecosome species I have observed. Hand shading applied to change the illumination on a feeding individual elicits no escape response unless associated with turbulence.

I have observed *Cavolina uncinata* (Rang), *C. tridentata* (Niebuhr), *C. longirostris* (Blainville), *C. inflexa* (Lesueur) and *Diacria quadridentata* (Blainville) withdraw feeding webs, and then enter a non-fishing period that lasts for observed periods of up to 12 min. During this period, no web is present but pseudofeces and fecal pellets are transported down the dorsal surface and are retained posteriorly (Fig. 1d), as described previously (Gilmer and Harbison, 1986). Photographs of *C. uncinata, C. tridentata* and *D. quadridentata* suggest they occupy one position long enough to set, fish, and ingest at least two webs. Figure 1c shows a specimen of *C. uncinata* with a web in place, but with no fecal matter or pseudofecal strings hanging from the posterior shell surface. Figure 1d shows another individual of this species with a web in place, but with fecal matter and pseudofecal strings present. This indicates a web was ingested and a new one set without swimming to a new location.

Particle laden webs of five *Cavolinia tridentata* were observed during dives in northwestern Atlantic slope water. Four specimens left webs in place for five minutes, and one withdrew the web after three minutes, possibly because of diver turbulence. The latter specimen required almost one minute to withdraw its web. All individuals appeared to have produced webs in the same locations previously as fecal and pseudofecal material were present. These observations suggest *Cavolinia* and *Diacria* can remain in one location for at least 35 min to set and fish sequential webs for five min each, and digest each web during 12 min "non-fishing" periods. Occasionally a combined mass of fecal pellets and pseudofeces can be indentified *in situ* though I have never observed an intact abandoned web without having first disturbed an animal.

All cavoliniid genera display the same somersaulting behavior as described for *Limacina* (Fig. 2). I have also observed an extended pattern of this behavior by several specimens of *Creseis acicula* (Rang) and *Cavolinia longirostris.* Initially, these individuals are motionless in feeding postures, but then sink away rapidly (approximately 5 cm/sec) for no apparent reason. After sinking 0.5 to 1.0 m, they somersault and again remain motionless. The somersault behavior in-

Table 1. Comparison of maximum dimensions of shells and feeding webs (in mm) of euthecosome species by region in the North Atlantic (includes data from Gilmer and Harbison, 1986).

Species	Location	Shell length (± S.D.)	Max. Web Diameter	
Limacina helicina	subarctic Atlantic	12.2 (diameter)	60	(24/3)
	McMurdo Sound, Antarctica	4.6 (diameter)	20	(3/1)
Cuvierina columella	north central Atlantic	11.0*	120	(13/5)
	slope water N.W. Atlantic	11.0*	110	(5/3)
Clio pyramidata	north central Atlantic	10.0 ± 0.4	50	(10/8)
	slope water N.W. Atlantic	10.0	40	(5/2)
Cavolinia longirostris	north central Atlantic	5.4	40	(7/3)
	northern Sargasso Sea	5.0 ± 0.2	40	(5/1)
	Gulf Stream axis	5.6	50	(2/1)
	slope water N.W. Atlantic	5.8	40	(3/2)
C. uncinata	northern Sargasso Sea	7.0	100	(7/2)
	Gulf Stream axis	7.0	110	(9/5)
	slope water N.W. Atlantic	7.0 ± 0.2	110	(3/3)
C. tridentata	north central Atlantic	15.0	180	(2/1)
	northern Sargasso Sea	15.0	200	(1)
	Gulf Stream axis	15.4	200	(2/2)
	slope water N.W. Atlantic	15.0 ± 0.2	220	(6/4)
Diacria quadridentata	Gulf Stream axis	3.0	30	(2/2)
	slope water N.W. Atlantic	3.0	20	(2/1)
	Canary Current	3.6	20	(3/1)

( ) No. of webs measured/No. with maximum dimension
* excludes shell posterior to caudal septum
** visual estimation

volves the only swimming activity. I have observed several individuals each sink and somersault in this sequence up to four times in five min, with a net descent of approximately 3 m. At the end of this sequence the animal either remains motionless with no apparent web for the duration of the observation (up to five min), or swims off in a random direction out of the diving grid (>20 m).

Small crustaceans often hover around feeding cavoliniids (Gilmer and Harbison, 1986), apparently attracted to the various surfaces as reported for larvacean mucous houses (Alldredge, 1972). During nighttime observations of *Cavolinia uncinata* (n=3), *Clio pyramidata* (n=15), and *Cuvierina columnella* (N=18), crustaceans (<1 mm length) were usually observed inside the web as it was ingested. Initially, the crustaceans were free swimming inside the spherical web area, but some appeared to be captured in the mucous walls as the web was withdrawn. Four specimens I observed and collected at night each had an estimated 20 to 30 crustaceans trapped in their webs as they withdrew them, and all had crustaceans in their guts (Table 2). Only smaller crustaceans are successfully captured. Hyperiid amphipods (3 to 4 mm) attracted by the dive lights were often caught in the webs, but easily broke free after several rapid swimming motions.

Species occupying different water masses of the north Atlantic do not appear to alter their maximum web dimensions (Table 1). *Cavolinia tridentata*, *C. longirostris,* and *C. uncinata* were each observed with webs of similar dimension in central water masses of the temperate North Atlantic, the northern Sargasso Sea, the axis of the Gulf Stream, and in slope water along the northwestern Atlantic coast.

FAMILY CYMBULIIDAE (PSEUDOTHECOSOMATA)

The cymbuliids feed with enormous mucous webs that are often observed funnelled towards the footlobes as the animal lies below the web (Fig. 1e). Observations of *Corolla* and *Gleba* indicate that the web is slowly drawn in by the footlobes surrounding the mouth rather than the rapid, deflating balloon method observed with the spherical webs of euthecosomes. I have observed large numbers of *Corolla* calceola (Verrill) feeding in slope water regions of the northwest Atlantic. No apparent change in web size occurs during observations lasting up to 15 minutes. Food is ingested continuously and pseudofeces are released as long strands off the anterior side of the footlobes (see Lalli and Gilmer, 1989 for orientation in pseudothecosomes). I observed one specimen heavily laden with mucus and pseudofeces (Fig. 1f), suggesting that it had recently ingested a web. The mucus contained many copepods, larvaceans, and small diphyiid siphonophores in addition to the waste matter. It actively swam twelve meters horizontally before freeing itself from the mucus, and then swam downwards out of our diving range (>30 m). I have no observations to indicate whether cymbuliids ever set sequential webs in one location.

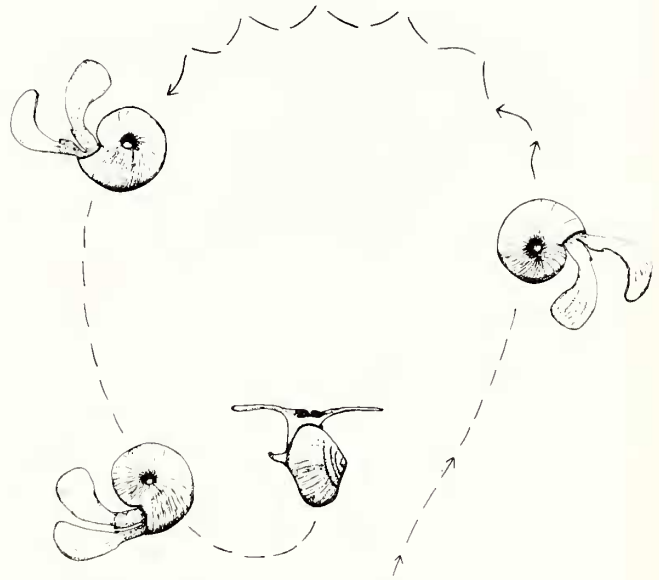## DISCUSSION

Among oceanic suspension feeders that employ

Fig. 2. Somersaulting behavior by *Limacina helicina* which occurs at the initiation of the motionless feeding posture. A similar behavior is displayed by all euthecosome genera.

mucous structures, thecosomes appear to feed by a novel trapping strategy. Although some larvaceans (Alldredge, 1976) and all doliolids (Diebel, 1982) share a motionless feeding posture with thecosomes, these tunicates pump water through their mucous filters and feed on very small particles. Salps feed in a manner more analogous to thecosomes, but move constantly with pumping motions and expose their feeding webs to continuous new water (Madin, 1974; Harbison and Gilmer, 1976). Whether thecosomes remain in one location or sink slightly during feeding, they use no active transport of water through the web as in tunicates. Thecosomes appear well suited to feeding by contract trapping of large motile organisms based on the occurrence of numerous crustaceans in and around the webs and in the gut contents of carefully collected specimens.

Although nighttime observations are the most limited in number, they have provided the most information about the trapping ability of the thecosome webs. All individuals I have closely observed feeding at night (n=35) capture numerous small crustaceans as they withdraw the web. The few specimens also collected during these dives have all had small copepods in their guts (Table 2). These observations remain qualitative, since much of the web material and potential food was undoubtedly lost during the capture. Intact crustaceans account for up to 25% by volume of intact items in guts of arctic *Limacina helicina* preserved *in situ* (Gilmer and Harbison, unpub. data). Copepods, however, are entirely absent in the laboratory for as little as three hours after capture. Small fragments of copepod exoskeleton are common in fecal pellets of *L. helicina*, especially segments of endopodites and thoraces.

The estimated times for *Cavolinia* and *Diacria* to fish two webs is limited by my short observation periods. The actual fishing times and the number of webs set in any one

Table 2. Gut contents of cavoliniids collected on night dives with crustaceans observed inside their feeding webs.

Species (Locality)	Dominant taxa	Max. dimension (μm)		No. of food items
Cuvierina columnella (n=2)	copepod naupli	thorax	<600	5
	tintiniids	lorica	120	14
(Northern Sargasso Sea)	thecate dinoflagellates		60	18
	Globigerina spp.		120	3
	centric diatoms		30	24
Clip pyramidata (N=1)	copepod juvenile	thorax	1100	1
	copepod nauplii	thorax	<600	4
(Northern Sargasso Sea)	tintiniids	lorica	110	21
	Radiolarians		150	4
	centric diatoms		30	4
Cavolinia uncinata (n=1)	copepod nauplii	thorax	<700	3
	Limacina inflata juv.	shell	<300	2
(Florida Current)	tintinnids	lorica	140	6
	thecate dinoflagellates		90	7

location are undoubtedly much greater, judging from the extensive amount of pseudofeces that some individuals accumulate. This quiescent behavior may explain how well developed hydroid colonies exist on the shells of some thecosomes. *Kinetocodium danae* Kramp often found on *Diacria trispinosa* (Blainville) (Lalli and Gilmer, 1989) has feeding polyps that could easily reach the web surface to prey upon attracted crustaceans. Hydroids I have observed on other thecosomes have feeding polyps either situated near the anterior portion of the shell, nearest the host feeding web, or have stalked feeding polyps that could reach the host web from other regions of attachment on the shell.

The large, sheet-like webs used by pseudothecosomes and the slow methodical fashion of ingesting them is easily comparable to the feeding style of the vermetid prosobranchs (Hughes and Lewis, 1974; Hughes, 1978). In contrast, the spherical webs used by euthecosomes and their ability to rapidly ingest them appears to be unique among marine animals that feed with mucous structures.

Much of the feeding behavior of thecosomes remains obscure. For instance, webs produced by *Limacina* appear to arrest sinking and provide neutral buoyancy during feeding, although mating couples display neutral buoyancy as well and have no feeding webs in place. Secondly, the somersaulting action displayed by all euthecosomes does not appear to coincide with the setting of a web, but always occurs prior to initiation of the feeding posture. Finally, it is unclear how free swimming copepods penetrate the walls of the euthecosome webs without adhering to them. Hopefully, future *in situ* observations and collections will help to answer these questions and may ultimately help determine the precise, thecosome feeding strategy.

ACKNOWLEDGMENTS

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